Individual variation in metabolic reaction norms over ambient temperature causes low correlation between basal and standard metabolic rate

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RESEARCH ARTICLE

Individual variation in metabolic reaction norms over ambient temperature causes low correlation between basal and standard metabolic rate

Michael Briga*,‡ and Simon Verhulst

ABSTRACT

Basal metabolic rate (BMR) is often assumed to be indicative of the energy turnover at ambient temperatures (T_a) below the thermoneutral zone (SMR), but this assumption has remained largely untested. Using a new statistical approach, we quantified the consistency in nocturnal metabolic rate across a temperature range in zebra finches (N=3213 measurements on 407 individuals) living permanently in eight outdoor aviaries. Foraging conditions were either benign or harsh, and body mass and mass-adjusted BMR (BMR_m) and SMR (SMR_m) were lower in individuals living in a harsh foraging environment. The correlation between SMR_m at different T_a was high (r=0.91), independent of foraging environment, showing that individuals are consistently ranked according to their SMR_m. However, the correlations between BMR_m and SMR_m were always lower (average: r=0.29; range: 0<r<0.50), in particular in the benign foraging environment. Variation in metabolic response to lower T_a at least in part reflected differential body temperature (T_b) regulation: early morning T_b was lower at low T_a, and more so in individuals with a weaker metabolic response to lower T_a. Our findings have implications for the use of BMR in the estimation of time–energy budgets and comparative analyses: we suggest that the use of metabolic rates at ecologically relevant T_a, such as the easily tractable SMR, will be more informative than the use of BMR as a proxy for energy turnover.

KEY WORDS: BMR, SMR, Repeatability, Foraging, Daily energy expenditure, Body temperature

INTRODUCTION

Energy is an essential resource for reproduction and survival (Boutin, 1990; Martin, 1987; Prevedello et al., 2013; Ruffino et al., 2014). The energy an individual spends daily on all activities is called the daily energy expenditure (DEE) and includes all processes such as self-maintenance, thermoregulation and behaviour. Measuring DEE is highly relevant but often practically demanding. A component of energy turnover that is more tractable and often quantified is basal metabolic rate (BMR), i.e. the minimum energy expenditure of a post-absorptive adult animal measured during the rest phase at thermoneutral temperature (IUPS Thermal Commission, 2001; McNab, 1997). Thermoneutral temperature is defined as the ambient temperature (T_a) at which body temperature (T_b) regulation is achieved without regulatory changes in metabolic heat production or evaporative water loss (IUPS Thermal Commission, 2001). BMR has been studied in association with many traits such as growth, reproduction, personality, oxidative stress, senescence and survival (reviewed in Biro and Stamps, 2010; Burton et al., 2011; Glazier, 2015). It is often implicitly assumed that individual variation in BMR is representative of individual variation in DEE. However, the correlation between DEE and BMR is generally weak in birds and mammals ($0<R^2<0.23$; Careau et al., 2012; Fyhn et al., 2001; Meerlo et al., 1997; Speakman et al., 2003; Tieleman et al., 2008; Wiersma and Tinbergen, 2003). Thus, the assumption that individual variation in BMR reflects variation in DEE, and hence can be interpreted as an index of total energy turnover, is not well supported.

Multiple hypotheses can be formulated to explain why BMR and DEE are only weakly correlated. The hypothesis we investigated here is that the low correlation between BMR and DEE is at least in part due to the fact that BMR is measured at thermoneutrality, while DEE is measured at T_a as experienced in natural environments, which are often below thermoneutrality. As BMR represents a considerable proportion of an individual's energy expenditure (~30%; e.g. Careau et al., 2012; Daan et al., 1990), we would expect a positive association between BMR and standard metabolic rate (SMR), i.e. metabolic rate below thermoneutrality but otherwise in identical conditions. However, SMR is more influenced than BMR by T_b and insulation. These could associate positively with BMR, for example because individuals with poor insulation need an enhanced thermoregulatory machinery to maintain T_b, causing an indirect positive association between BMR and SMR. Conversely, T_b and insulation might differ between individuals to such an extent that BMR and SMR will correlate poorly. To the best of our knowledge, the association between BMR and SMR remains unknown. To investigate individual variation in this relationship, we repeatedly measured BMR and SMR in a small passerine, the zebra finch, in the same individuals and under the same conditions except that T_a was below the thermoneutral zone during SMR measurements. If individual differences in thermoregulatory response to a lower T_a are small relative to the average response, individual variation in BMR will be strongly correlated with SMR. In this case, BMR and SMR can be considered different expressions of the 'same' trait. Alternatively, individuals may differ in their thermoregulatory response to the extent that the correlation between BMR and SMR is weak or absent. In this case, BMR and SMR are uncoupled and this would at least partly explain the low correlations observed between BMR and DEE.

When multiple traits of an individual are measured multiple times, phenotypic correlations between traits can arise via two ways

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List of abbreviations

BMR	basal metabolic rate
BMR_m	mass-adjusted basal metabolic rate
DEE	daily energy expenditure
MMR	maximum metabolic rate
SMR	standard metabolic rate
SMR_m	mass-adjusted standard metabolic rate
T_a	ambient temperature
T_b	body temperature

(Fig. 1). Firstly, individual mean values of trait A may correlate with individual mean values of trait B, which we here define as between-individual correlations. Secondly, the change over time in trait A may correlate with the change in trait B in that same individual, which we here define as within-individual correlations (following Dingemanse and Dochtermann, 2013). Because correlations at the two levels reflect biologically distinct processes, we decomposed the phenotypic correlations between BMR and SMR into between- versus within-individual correlations. Because we were mostly interested in differences between individuals, we discuss here mainly between-individual correlations.

Potential correlations between variables are affected by the variables' repeatability. For example, when repeatability of a trait is zero, between-individual correlations with that trait will also be zero. Furthermore, repeatability is relevant in evolutionary terms because consistent differences between individuals are a minimum requirement for natural selection to act upon (Falconer and Mackay, 1996). Hence, here we first quantified the repeatability of body mass, BMR and SMR of zebra finches at T_a ranging from 5 to 39°C (Fig. 2). We then investigated the within- and between-individual correlations between metabolic rates at different T_a. When exposed to a lower T_a, homoeothermic organisms balance three interrelated physiological factors: metabolic rate, insulation and T_b (Geiser, 2004; McNab, 1980). For example, large differences between T_a

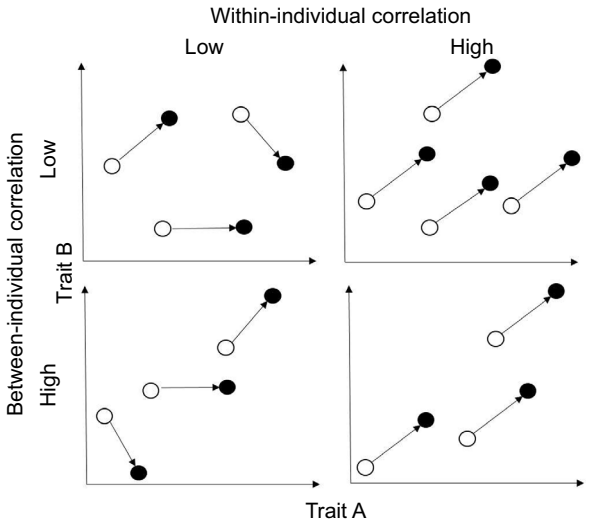

Fig. 1. Graphic representation of between- and within-individual correlations for two traits A and B. Each arrow represents an individual with a first and second measurement (open and filled circles, respectively). A high between-individual correlation means that individual mean values of trait A correlate with individual mean values of trait B (bottom two illustrations). A high within-individual correlation means that for a particular individual the change in value of trait A correlates with the change in value of trait B (i.e. arrows are in similar directions for all individuals, illustrations on the right).

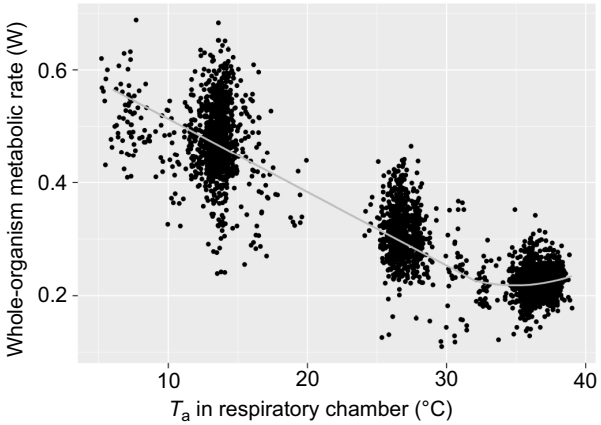

Fig. 2. Metabolic rate declines with increasing ambient temperature (T_a) until the thermoneutral zone between 32 and 39°C. Data are consistent with the classic results of Scholander et al. (1950) and Calder (1964). The grey line shows the fit. *N*=3213 measurements from 407 individuals.

and T_b increase heat loss, and one way to minimize this loss is by down-regulating T_b (Angilletta et al., 2010; Geiser, 2004; Körtner et al., 2000). Thus, T_b adjustments can be an important determinant of metabolic responses to lower T_a. To investigate the role of temperature regulation, we measured T_b of a subset of individuals at multiple T_a and correlated individual metabolic reaction norms over T_a with changes in T_b.

Repeatability and trait correlations are inherently specific to a population and its environment. The birds used in this study lived in captivity, which may alter metabolism and possibly its repeatability relative to that of free-living animals (e.g. Auer et al., 2016). One essential difference between captive and free-living populations is that food can usually be accessed at negligible costs in captivity, which is not usually true for free-living animals (Beaulieu, 2016; Briga and Verhulst, 2015a), and this can have physiological and demographic consequences (e.g. Briga et al., 2017; Robb et al., 2008). To broaden the range of environments and increase the ecological relevance of our study, we housed the birds in outdoor aviaries, and permanently exposed half of our population to high foraging costs through a manipulation of flight cost per food reward (Koetsier and Verhulst, 2011). Increased foraging costs generally result in lower BMR (reviewed in Wiersma and Verhulst, 2005), and in zebra finches this effect was stronger at lower temperatures, i.e. on SMR (Wiersma and Verhulst, 2005). However, whether foraging costs affect the association between BMR and SMR is unknown. Thus, we experimentally manipulated foraging costs and compared BMR and SMR repeatability and correlations in a 'benign' environment versus a 'harsh' semi-natural environment.

MATERIALS AND METHODS

Birds and housing

The birds we studied are part of a long-term experiment investigating the relationships between foraging costs and survival (Briga and Verhulst, 2015b; Briga et al., 2017). Birds were housed in eight unisex outdoor aviaries (L×W×H: 320×150×225 cm) located in Groningen, The Netherlands (53°13′0″N, 6°33′0″E). Foraging costs were manipulated as described by Koetsier and Verhulst (2011). In brief, in each aviary a food box was attached to the ceiling, with holes in the sides from which food (tropical seed mixture) could be obtained. In the benign foraging environment (four aviaries) the food box had perches beneath the holes, while in the harsh foraging environment (also four aviaries) these were

Journal of Experimental Biology (2017) 220, 3280-3289 doi:10.1242/jeb.160069

removed, forcing birds to fly and hover for seeds. Water, grit and cuttlebone were provided *ad libitum* and birds received 1.25 g of fortified canary food ('eggfood', Bogena, Hedel, The Netherlands) per individual per week given in three portions. Each aviary contained an approximately equal number of birds (15–25) and we kept bird density within a limited range by regularly adding birds to replace those that died. All birds had been reared in either small or large broods with in most cases two or six young. The manipulated brood sizes were within the natural range for zebra finches in the wild (Zann, 1996) and in captivity (Griffith et al., 2017). The brood size manipulation did not affect mass-adjusted BMR/SMR (Briga, 2016) and will therefore not be further considered here. All methods and experimental protocols were carried out under the approval of the Animal Experimentation Ethical Committee of the University of Groningen, licence 5150A. All methods were carried out in accordance with these approved guidelines.

Body mass and body size

Between December 2007, when the experiment started, and December 2015, we collected 15,443 mass measurements on 597 individuals. Birds were weighed almost monthly, up to 95 times (Fig. S1A) between the ages of 0.4 and 9.4 years. We used this whole dataset to estimate treatment effects. However, to consistently estimate repeatability, within- and between-individual variances (see below) based on the same individuals, we selected those individuals with at least two measurements (N=15,418 measurements on 572 individuals). Size measurements, tarsus and head+bill, were taken after reaching maturity, on average at age 133±33 days (mean±s.d.), and averaged after transformation to a standard normal distribution to obtain one estimate of structural body size.

Metabolic rate

Overnight energy expenditure was measured using an open-flow respirometer situated in a dark climate-controlled room kept at the desired T_a. Up to 16 individuals per night were taken from the aviaries on average at 18:10 h (±1:17 h s.d.), weighed (±0.1 g) and randomly assigned to one of 16, 1.5 l metabolic chambers in a dark climate room. Measurements lasted until the morning, such that birds were in a post-absorptive state, thus meeting the requirements for BMR (IUPS Thermal Commission, 2001; McNab, 1997) and this was consistent for SMR as well. Rooms were kept and continuously monitored at the above-mentioned temperatures with multiple PT100 temperature sensors, one located in the room recording continuously and one in each metabolic chamber recording at each metabolic rate measurement. Technical specification of the equipment can be found in Bouwhuis et al. (2011). In brief, the air flow through the metabolic chambers was controlled at 25 l h^{-1} by mass-flow controllers (5850S, Brooks, Rijswijk, The Netherlands) calibrated with a bubble flow meter. Air was dried using a molecular sieve (3 Å; Merck, Darmstadt, Germany) and analysed by a paramagnetic oxygen analyser (Servomex Xentra 4100, Crowborough, UK). During measurements, each metabolic chamber or reference outdoor air was sampled every 8 min for 60 s to stabilize measurement levels. In each sampling, we measured O_2 concentration and oxygen consumption was calculated using equation 6 of Hill (1972). An energy equivalent of 19.7 kJ l^{-1} oxygen consumed was used to calculate energy expenditure in watts. Metabolic rate was taken to be the minimum value of a 30 min running average, which included 3–6 measurements per individual. The first measurement hour was excluded to minimize potential effects of handling stress and the incomplete mixing of air in the metabolic chamber. Birds were weighed before and after the respirometry measurement and body mass for the metabolic rate analyses was taken to be the average of the two values.

Between December 2007 and April 2013, we collected 3213 metabolic rate measurements from 407 birds. Metabolic rate measurements were obtained at T_a ranging from 5 to 39°C (Fig. 2), but most measurements were centred on three T_a of 36°C (range 32–39°C, Fig. S2) for BMR and 26°C (±3°C) and 12°C (±3°C) for SMR (Table 1). We refer to the metabolic rates at these three T_a categories as BMR, SMR26 and SMR12, respectively. Measurements were concentrated in spring and autumn. Birds were measured up to 25 times (Fig. S1B) between the ages of 0.4 and 7.2 years. To estimate treatment and seasonal effects, we used this whole dataset, avoiding any possible bias by selecting data subsets. For the repeatability analyses, we used data subsets as described in Table 1. In brief, to estimate repeatability, within- and between-individual variances based on the same individuals and correlations, we selected those individuals with at least two measurements (Table 1).

T_b

During autumn–winter 2011, we measured T_b at the end of respirometry measurements (N=550; mean time 09:46 h, ±0:38 h s.d.) of 189 individuals using an Omega® Thermocouple Thermometer Type T smoothed with Johnson & Johnson® lubrication gel. Handling time during measurements was ≤30 s and the temperature reading was obtained within 5 s of the probe entering the cloaca, at which time T_b was stable. T_b increased as birds were subsequently measured in the climate-controlled room and hence we included measurement order as a covariate in all analyses. In analyses with T_b as predictor, we used order-adjusted values.

Statistical analyses

The repeatability is the proportion of phenotypic variance attributed to between-individual variance (Nakagawa and Schielzeth, 2010).

Table 1. Description of the metabolic rate dataset at ambient temperature (T_a) ranges for which most data were collected

	SMR12	SMR26	BMR
Whole population			
Temperature range (°C)	9–15	23–29	32–39
Date of first measurement	16 Apr 2008	19 Apr 2008	16 Dec 2007
Date of last measurement	12 Apr 2013	14 Apr 2013	15 Apr 2013
No. of birds	314	303	386
No. of birds with >1 measurement	214	210	275
No. of measurements	976	821	1233
Mean metabolic rate (W)	0.48	0.31	0.22
s.d. metabolic rate (W)	0.063	0.045	0.027
CV metabolic rate	0.13	0.15	0.12
Benign environment			
Date first measurement	18 Apr 2008	30 Jun 2008	16 Dec 2007
Date last measurement	9 Apr 2013	14 Apr 2013	15 Apr 2013
No. of birds with >1 measurement	110	107	133
No. of measurements	465	377	554
Harsh environment			
Date first measurement	24 Apr 2008	19 Apr 2008	18 Dec 2007
Date last measurement	12 Apr 2013	13 Apr 2013	6 Apr 2013
No. of birds with >1 measurement	104	103	143
No. of measurements	411	351	569

Note that the whole dataset is larger and includes measurements at other T_a than the intervals considered here (Fig. 2). SMR, standard metabolic rate (measured at 12 or 26°C); BMR, basal metabolic rate; CV, coefficient of variation.

Journal of Experimental Biology

Journal of Experimental Biology (2017) 220, 3280-3289 doi:10.1242/jeb.160069

These variance components can be estimated using a linear mixed model in which the between-individual variance is captured by including individual identity as a random effect and in which the phenotypic variance is the sum of the between-individual variance and the residual variance. In such models, residual variance decreases by including fixed effects, thereby increasing repeatability. Body mass repeatability estimates did not include fixed effects except when adjusting for size. Metabolic rate repeatability estimates included as linear fixed effects T_a and, for mass-adjusted estimates, mass. Variance components were estimated using a Bayesian approach (Dingemanse and Dochtermann, 2013) with the R package MCMCglmm (Hadfield, 2010) in R (www.R-project.org) with flat improper priors with 1.5×10^5 iterations, 10,000 burn-in and a thinning interval of 100. This yielded Markov chain Monte Carlo (MCMC) sample sizes of at least 1000 with low levels of autocorrelation (mean $r=-0.002$ with all $r<0.1$). Bayesian results were consistent with those of the frequentist approach (with restricted maximum likelihood and maximum likelihood; results not shown), using the functions (i) lmer of the package lme4 (Bates et al., 2015), (ii) lme of the package nlme (https://CRAN.R-project.org/package=nlme) and (iii) rpt of the package rptR (Nakagawa and Schielzeth, 2010). We here report Bayesian estimates with 95% credible intervals (CI). To test for significance of repeatability, we used likelihood ratio tests with the function exactLRT in the package RLRsim (Scheipl et al., 2008). To test for differences between repeatabilities, we used *t*-tests with the number of individual identities as (conservative) sample size. Covariation between traits was analysed using a Bayesian approach with a trivariate analysis (SMR12, SMR26 and BMR) with the function MCMCglmm (Hadfield, 2010) using uninformative inverse Wishart priors. In these models, metabolic values were residuals of a linear model with mass and T_a as fixed effects and with individual identity as a random effect. Repeatability and trait correlations for different foraging treatments were estimated separately by selecting data subsets. The effects of the season and foraging cost manipulation were analysed using general linear mixed models, lmer of the package lme4 (Bates et al., 2015) including individual as random effect. Residuals of all models were checked with function resid and all had a normal distribution without outliers. Effect sizes are reported as Cohen's *d* (Cohen, 1988), which was estimated as the ratio of the coefficient over the trait's standard deviation (equations 1 and 2 in Nakagawa and Cuthill, 2007). As a rule of thumb, effect sizes of 0.5 are considered as moderate (Cohen, 1988) and this was also the median effect size estimated from 43 ecological or evolutionary studies (Moller and Jennions, 2002).

RESULTS

Body mass repeatability

Repeatability of body mass was high at 0.72 (0.69<95% CI<0.74; Fig. 3B; N=15,418 measurements on 572 individuals). Body mass increased with size (r=0.56), and a modest part of the between-individual variation was due to variation in body size: body mass repeatability adjusted for size was 0.12 lower at 0.60 (0.57<95% CI<0.63; Fig. 3B). All estimates were significantly larger than zero (LR>11,324; $P<10^{-15}$). Hence, the zebra finches in our population can be characterized by their body mass and size-adjusted body mass.

Birds exposed to high foraging costs weighed on average 15.0 g, which was 4% (0.64 g, effect size d=0.41) lighter than birds with low foraging costs (Fig. 3A; $F_{1,580}$=43, $P<10^{-8}$), and this difference persisted when controlling for size ($F_{1,471}$=44, $P<10^{-10}$). Thus, high foraging costs negatively affected body mass.

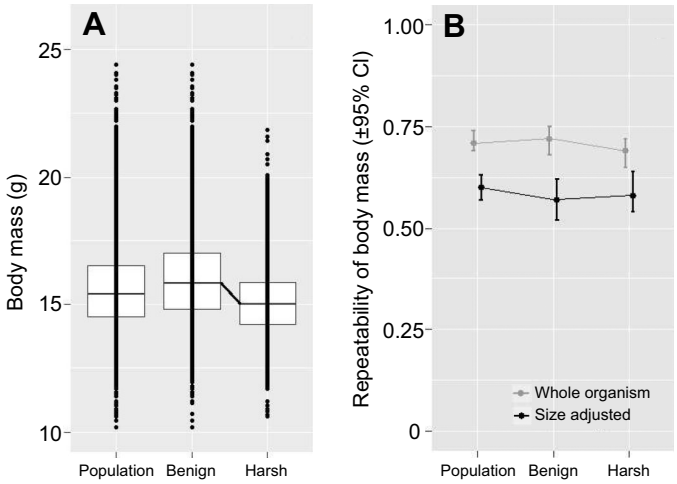

Fig. 3. Environmental quality affects body mass but not its repeatability. (A) Body mass. (B) Repeatability of body mass, presented ±95% credible interval (CI). 'Population' refers to all the birds pooled; 'Benign' and 'Harsh' refer to the subset of the population that lived in either the benign or harsh environment (low and high foraging cost, respectively). Boxplots show median, 25–75 and 5–95 percentiles (black vertical lines) and points outside this range. Repeatability estimates are based on the between- and within-individual variances in Table S1. Note, the smaller body mass range in the harsh environment in A, which was due to smaller within- and between-individual variance (Table S1).

Environmental conditions can affect between- and within-individual variance of traits, potentially making repeatability values conditional on the environment. The mass of birds living with high foraging costs was characterized by smaller between- and within-individual variance relative to birds living with low foraging costs (Table S1; t_{469}>2.56, P<0.011). However, between- and within-individual variance components changed to the same extent, and hence repeatability estimates of body mass and size-adjusted body mass were similar in the two environments (~0.70 and 0.60, respectively; Fig. 3B). Thus, environmental quality did not affect the repeatability of body mass, but individuals in a harsh environment experienced smaller body mass variation between and within individuals.

Metabolic rate repeatability

Metabolic rate decreased from 5 to 32°C (Fig. 2), consistent with the classic literature (Scholander et al., 1950). Note that with decreasing metabolic rate, s.d. also decreased (Table 1). This decrease in s.d. was proportional to the decrease in mean value as the coefficients of variation remained similar across all T_a (Table 1). Between 32 and 39°C, metabolic rate was steady (Fig. 2). We identified this T_a range as the zebra finches' thermoneutral zone (Fig. S2), confirming earlier results (Calder, 1964) with a 10-fold larger dataset. Thus, the associations between metabolic rate and T_a were consistent with those described in the classic literature.

Repeatability of whole-organism BMR was 0.54 (0.47<95% CI<0.58; LR=379, $P<10^{-15}$; Fig. 4B; Table S2), within the range of previously published results (Nespolo and Franco, 2007; Versteegh et al., 2008; White et al., 2013). Whole-organism metabolic rate is to a large extent determined by body mass (r=0.61). When body mass was added to the statistical model, repeatability of mass-adjusted BMR (BMR_m) was halved to 0.27 (0.22<95% CI<0.35; LR=94, $P<10^{-15}$; Fig. 4B; Table S2). Similarly, for SMR, the repeatability of whole-organism values was 0.39 (0.33<95% CI<0.43; LR=451, $P<10^{-15}$), which was larger than that for mass-adjusted values (SMR_m), which was 0.28 (0.24<95% CI<0.35; LR=248, $P<10^{-15}$;

Journal of Experimental Biology

Journal of Experimental Biology (2017) 220, 3280-3289 doi:10.1242/jeb.160069

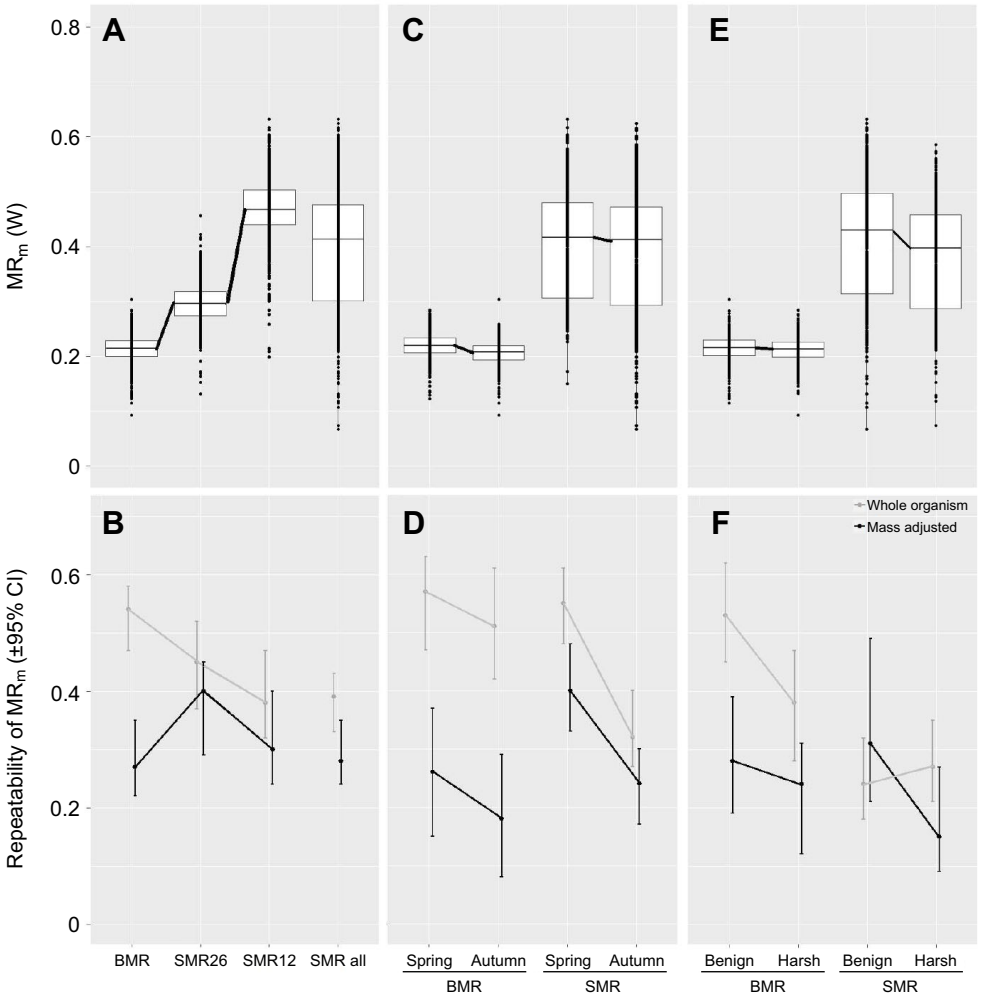

Fig. 4. Mass-adjusted metabolic rate (MR_m) and its repeatability for different subsets of the data. MR_m increased at lower T_a (SMR at 12 versus 26°C; A), but individuals can be equally well characterized by their mass-adjusted basal metabolic rate (BMR_m) as by their mass-adjusted standard metabolic rate (SMR_m; B). MR_m and its repeatability were higher in spring than in autumn (C,D) and in benign than in harsh environments (E,F). Mass-adjusted values were estimated for the population mean body mass of 15.13 g. Boxplots show median, and 25–75 and 5–95 (black vertical lines) percentiles. Differences in repeatability estimates can arise as a result of changes in either between- or within-individual variance; these are summarized in Table S2.

Fig. 4B; Table S2). The repeatability of BMR_m and SMR_m was very similar at 0.27 and 0.28, respectively (Fig. 4B; Table S2). For SMR_m within narrower T_a ranges (SMR_m12 and SMR_m26), the repeatability was slightly higher at 0.30 and 0.40, respectively (Fig. 4B; both LR>102, $P<10^{-15}$). Thus, the zebra finches in our population can be characterized by their BMR_m as well as by their SMR_m. Because the high repeatability of body mass often inflates metabolic rate repeatability (Fig. 4B,D,E), we further discuss results for mass-adjusted values only. Whole-organism results were mostly identical (results not shown).

In accordance with earlier studies in non-migratory birds (McKechnie, 2008), we found BMR_m and SMR_m to vary seasonally. BMR_m and SMR_m were, respectively, 0.011 and 0.025 W g^{-1} higher in spring than in autumn (Fig. 4C; BMR_m: $F_{1,1001}$=108, $P<10^{-15}$; SMR_m: $F_{1,1880}$=153, $P<10^{-15}$), or an effect size d=0.5 for both traits. Seasonal mass-adjusted metabolic rate change within individuals may exceed that between individuals (e.g. Bouwhuis et al., 2011). This would result in higher metabolic rate repeatability within season (in different years) compared with the mass-adjusted metabolic rate repeatability estimated with seasons pooled. For BMR_m, spring and autumn repeatability were within the same range as year-round repeatability (0.26 and 0.18 versus 0.27, respectively; Fig. 4D; t_{443}<1.46, P>0.14). For SMR_m, autumn repeatability was within the same range as year-round repeatability (0.24 versus 0.28; Fig. 4D), but spring repeatability was higher (0.40; Fig. 4D; t_{539}=2.6, P<0.0095). Thus, birds showed seasonal adjustments in metabolic rate and these adjustments were consistent between individuals except for SMR_m in spring.

Increases in foraging effort often lead to energy-saving decreases in BMR_m (reviewed in Wiersma and Verhulst, 2005). Indeed, BMR_m and SMR_m were lower in birds experiencing higher foraging costs (Fig. 4E; BMR_m: $F_{1,338}$=28, $P<10^{-6}$; SMR_m: $F_{1,271}$=82, $P<10^{-15}$), with the effect being more pronounced on SMR_m (0.030 W g^{-1} or an effect size d=0.60) than on BMR_m (0.009 W g^{-1} or an effect size d=0.42; Fig. 4E; $F_{1,3002}$=112, $P<10^{-15}$). The negative effect of foraging costs on SMR_m also became more pronounced at lower T_a ($F_{1,1692}$=4.7, P=0.03). Thus, birds from harsh environments lowered their minimal energy expenditure, and this became more pronounced with colder T_a.

Repeatability of BMR_m and SMR_m was, respectively, 23% and 48% higher in the low foraging cost environment than in the high foraging cost environment (BMR_m: 0.26 versus 0.20; SMR_m: 0.31 versus 0.16; Fig. 4F; Table S2), but these differences were at best marginally significant (t_{309}<1.83, P>0.07). For BMR_m, the lower repeatability arose as a result of lower between-individual variance in the high foraging cost environment, while the within-individual variance was environment independent (Table S2). For SMR_m, the high foraging cost birds were characterized by lower between- and within-individual variance, but none of these patterns were significant (Table S2; t_{309}<1.60, P>0.11). Thus, birds in a benign environment had a higher repeatability of metabolic rate, but the effect of environment was not significant.

Journal of Experimental Biology

Journal of Experimental Biology (2017) 220, 3280-3289 doi:10.1242/jeb.160069

Table 2. Correlations (±95% credible interval) between mass-adjusted metabolic rates at multiple levels

	Correlation level		
	Overall phenotypic	Between individual	Within individual
Whole population			
SMR_m12–SMR_m26	0.43 (0.36–0.49)	0.91 (0.79–0.98)	0.12 (0.02–0.22)
BMR_m–SMR_m12	0.14 (0.06–0.22)	0.37 (0.11–0.57)	0.04 (−0.06–0.15)
BMR_m–SMR_m26	0.22 (0.14–0.29)	0.34 (0.02–0.51)	0.20 (0.10–0.31)
Benign environment			
SMR_m12–SMR_m26	0.36 (0.26–0.46)	0.89 (0.48–0.98)	0.25 (0.11–0.37)
BMR_m–SMR_m12	0.14 (0.03–0.25)	0.18 (−0.21–0.54)	0.11 (−0.03–0.27)
BMR_m–SMR_m26	0.12 (0.001–0.23)	−0.06 (−0.46–0.39)	0.16 (0.04–0.31)
Harsh environment			
SMR_m12–SMR_m26	0.19 (0.07–0.30)	0.80 (0.43–0.98)	0.04 (−0.13–0.14)
BMR_m–SMR_m12	0.05 (−0.06–0.17)	0.50 (−0.19–0.98)	−0.02 (−0.17–0.11)
BMR_m–SMR_m26	0.28 (0.17–0.38)	0.43 (−0.22–0.96)	0.27 (0.14–0.41)

See Fig. 1 and Introduction for explanation. Phenotypic correlations (see Fig. S3) are the combined outcome of between- and within-individual correlations.

Metabolic rate correlations and reaction norms at multiple T_a

The phenotypic correlation between SMR_m12 and SMR_m26 was moderate at 0.43 (Table 2; Fig. S3C; $t_{577}>11.45$, $P<10^{-15}$). Surprisingly, the phenotypic correlations between BMR_m and either SMR_m12 or SMR_m26 were substantially lower ($0.14<r<0.22$; Table 2; Fig. S3C; $t_{577}>3.46$, $P<0.0006$). These patterns were consistent in both foraging environments (Table 2). Thus, SMR_m values at different T_a correlate better with each other than with BMR_m.

Phenotypic correlations in datasets with multiple observations per individual are the combined result of between- and within-individual correlations (Fig. 1) and here we tease apart these components. The between-individual correlation between SMR_m12 and SMR_m26 was higher than the phenotypic correlation and remained close to 1 in both foraging cost groups ($0.80<r<0.91$; Table 2). In contrast, the within-individual correlation between SMR_m12 and SMR_m26 was low ($0.04<r<0.25$; Table 2) and significantly positive only in the low foraging cost group (Table 2). Hence, the phenotypic correlation between SMR_m12 and SMR_m26 arose as a result of high between-individual correlation. Thus, individuals can be ranked consistently by their mean SMR_m over the whole sub-thermoneutral T_a range (Fig. 5A).

In contrast with the findings for SMR_m12 and SMR_m26, correlations between BMR_m and any of the SMR_m values were weak and their 95% CI often overlapped with zero between and within individuals and in both foraging cost groups (Table 2). Hence, the weak phenotypic correlations between BMR_m and any of SMR_m values arose as a result of weak between- and weak within-individual correlations. Thus, the ranking of individuals according to their mean BMR_m differs from the ranking according to their mean SMR_m (Fig. 5A).

The high correlation between SMR_m12 and SMR_m26 indicates that individuals can be characterized by their metabolic rate reaction norms over sub-thermoneutral T_a. Statistically, an individual reaction norm can be quantified by a random slope. We hence ran a random slope model with SMR data, including T_a and mass as fixed effects and individual identity as a random effect and we quantified the random slope by nesting T_a in individual identity. Indeed, a random slope model fitted the data better than a random intercept model for both SMR ($\Delta AICc=-41$) and SMR_m ($\Delta AICc=-15$; Fig. 5B). Thus, metabolic reaction norms over sub-thermoneutral T_a varied significantly between individuals. The improvement in model fit by inclusion of random slopes was larger in the low foraging cost environment than in the high foraging cost environment (SMR: $\Delta AICc=-6.8$; SMR_m: $\Delta AICc=-3.3$). Thus, individuals can be characterized by their metabolic reaction norms over sub-thermoneutral T_a (Fig. 5B) and this is most pronounced in a benign environment.

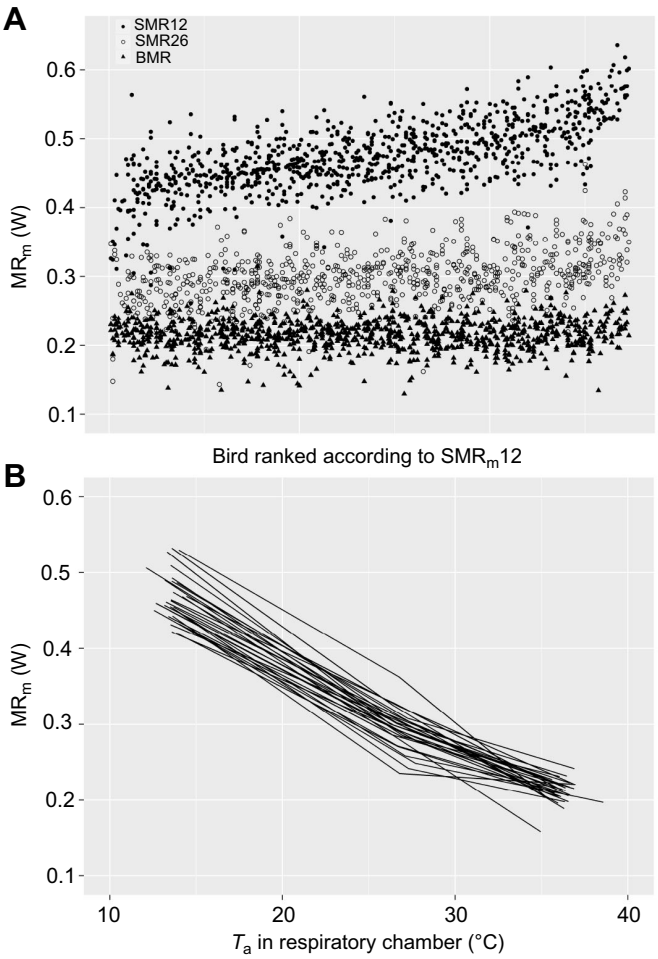

Fig. 5. SMR_m12 and SMR_m26 associate better with each another than with BMR_m. (A) Mass-adjusted metabolic rates of birds measured at three T_a (12, 26 and 36°C) and ordered along the *x*-axis according to increasing mass-adjusted metabolic rate at 12°C (SMR_m12). The consistent increase in metabolic rate to the right of the *x*-axis for SMR_m12 and for SMR_m26 illustrates their repeatability and between-individual correlation. This increase to the right is not present for BMR_m, showing its weak correlation with any of the SMR_m values. (B) Illustration of (mean) individual reaction norms for 30 randomly selected birds. Note that reaction norms appear more parallel below than above 32°C.

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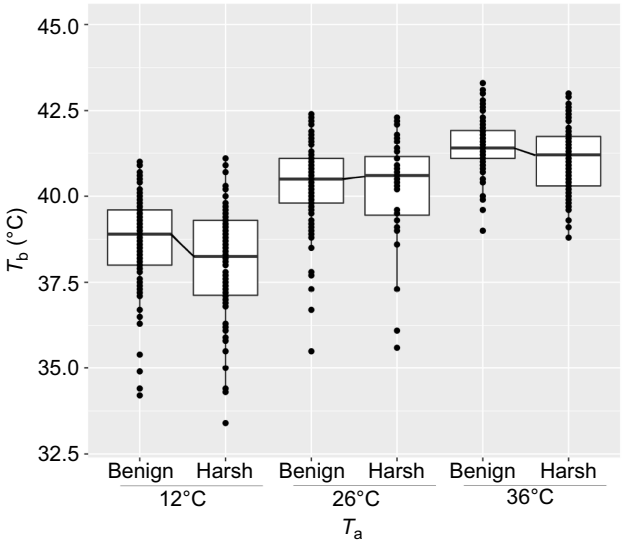

Fig. 6. T_b is lower at lower T_a and this is more pronounced for birds in the harsh foraging environment. Boxplots show median, and 25–75 and 5–95 (black vertical lines) percentiles, N=550 measurements on 189 individuals.

T_b

Birds decreased their T_b in response to lower T_a (Fig. 6; $F_{2,314}$=313, P<10^{-15}). Previous studies have shown that T_b is lower in individuals from harsh foraging environments (reviewed in Geiser, 2004; Vuarin and Henry, 2014). We confirmed this pattern at T_a=12°C (Fig. 6; $F_{1,133}$=9.24, P=0.0029) and at thermoneutral T_a (T_a=36°C; Fig. 6; $F_{1,147}$=9.22, P=0.0028), but not at T_a=26°C (Fig. 6; $F_{1,124}$=0.36, P=0.55). The environment×T_a interaction was significant ($F_{2,350}$=3.36, P=0.036). Thus, individuals in harsh environments maintained either the same or lower night-time T_b depending on T_a.

There are multiple solutions to balancing metabolic rate, insulation and T_b (McNab, 1980). Thermal physics predicts that, everything else remaining equal, individuals with low SMR_m also have a lower T_b (McNab, 1980). Indeed, this was the case at T_a=12°C (Fig. S4A; r=0.22; $F_{1,188}$=9.0, P=0.003). However, this association was absent at T_a=26°C (Fig. S4A; $F_{1,124}$=0.09, P=0.77) and for BMR (Fig. S4A; r=0.05; $F_{1,172}$=0.11, P=0.74). These results were consistent for both foraging cost groups ($F_{1,122}$<2.63, P>0.11). The difference in the association between T_b and mass-adjusted metabolic rate at different T_a values was significant ($F_{2,481}$=3.04, P=0.05), with the association becoming stronger with decreasing T_a.

We next investigated whether the weak between-individual correlation between BMR_m and SMR_m was associated with individual differences in T_b response to sub-thermoneutral T_a. We tested whether individual responses of mass-adjusted metabolic rate and T_b to colder T_a were correlated. Indeed, when comparing mass-adjusted metabolic rate and T_b between T_a of 36 and 12°C, individuals with the largest increases in mass-adjusted metabolic rate maintained the highest T_b (Fig. 7; r=0.21; $F_{1,121}$=5.46, P=0.02) for both foraging cost groups (Fig. 7; $F_{1,119}$=0.29, P=0.59). Between 26 and 12°C, we found a significant association for birds in the low foraging cost environment (Fig. S4B; $F_{1,59}$=7.45, P=0.008), but not for birds in the high foraging cost environment (Fig. S4B; $F_{1,41}$=0.16, P=0.69) and this difference was significant ($F_{1,101}$=4.34, P=0.04). Between 36 and 26°C, we found little evidence for positive association between mass-adjusted metabolic rate and T_b responses (Fig. S4C; r=−0.24; $F_{1,84}$=2.56, P=0.11). Hence, we found some evidence that when facing sub-thermoneutral T_a, some individuals maintain a higher mass-adjusted metabolic rate and T_b than others. Thus, the weak between-individual correlations between BMR_m and SMR_m (Table 2) are in part due to individual differences in T_b regulation in response to sub-thermoneutral T_a.

DISCUSSION

Body mass, BMR_m and SMR_m were repeatable traits in our study population (Fig. 3B, Fig. 4B). SMR_m at different T_a correlated almost perfectly between individuals (Table 2, Fig. 5A,B). In contrast, correlations between BMR_m and SMR_m were always weaker (Table 2, Fig. 5A,B). Thus, individuals with high BMR_m do not necessarily have high SMR_m and our results better fit the scenario in Fig. S3B over that in Fig. S3A. Individual variation in metabolic reaction norms can have various causes (McNab, 1980) and here we showed a role for differential T_b regulation: individuals with the steeper metabolic reaction norms maintained a higher T_b at low ambient temperatures (Fig. 7). Thus, BMR_m was a weak indicator of the energy turnover at sub-thermoneutral T_a and this was in part due to individual variation in T_b regulation.

Repeatability is likely to be environment specific, and thus the fact that our birds lived in captivity may have affected our findings. A major difference between captive and free-living populations is

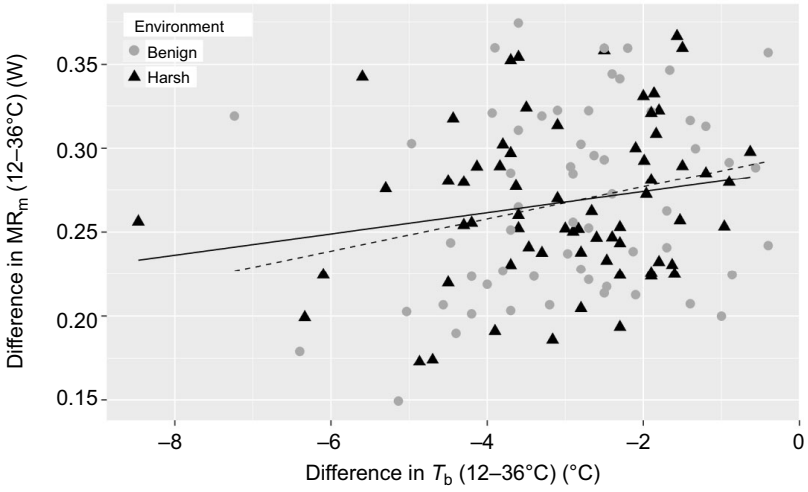

Fig. 7. Individuals with a smaller difference in metabolic rate between 12 and 36°C show a larger difference in T_b. Grey circles and dashed line show data and model fit for the benign environment; black triangles and continuous line show data and model fit for the harsh environment.

that food can often be accessed at negligible costs in captivity, which is not usually the case for free-living animals (e.g. Beaulieu, 2016; Briga and Verhulst, 2015a). To better mimic natural conditions, we therefore experimentally increased foraging costs, which decreased life expectancy up to 15% (Briga et al., 2017). A unique aspect of our study is that we carried out this manipulation for life, and hence our findings reflect long-term adjustments to foraging conditions. Individuals living with high foraging costs had lower body mass, BMR_m and SMR_m (Fig. 3A, Fig. 4A), consistent with shorter-term studies of birds (Bautista et al., 1998; Deerenberg et al., 1998; Koetsier and Verhulst, 2011; Wiersma and Verhulst, 2005) and mammals (Day and Bartness, 2001; Perrigo, 1987; Schubert et al., 2009; Vaanholt et al., 2007). The standardized effect size *d* of foraging costs on mass-adjusted metabolic rate was approximately 0.5, which appears a reasonably large effect (Moller and Jennions, 2002). However, to establish the biological significance of this finding, we need to know how the observed effect sizes translate into differences in lifespan and/or reproductive success.

The effect of increased foraging costs was more pronounced on SMR_m than on BMR_m, in agreement with the findings of Wiersma and Verhulst (2005). The increasing effect of foraging costs with lower temperature is probably due to increased use of energy-saving mechanisms at lower T_a, such as night-time hypothermia (Fig. 6), which appears to be a general response to increased foraging costs or food shortage (Angilletta et al., 2010; Daan et al., 1989; Geiser, 2004; McKechnie and Lovegrove, 2002; Vuarin and Henry, 2014). That more energy is saved when foraging costs are increased is not surprising, because an increase in thermoregulatory requirements leads to a knock-on increase in energy expenditure in hard foraging conditions, because more energy needs to be expended to gather the extra energy for thermoregulation. Thus, we predict that diurnal energy expenditure will increase faster in response to decreasing ambient temperature when foraging costs are high, but this remains to be tested.

Repeatability

The repeatability of whole-organism metabolic rate in the range 0.4–0.5 found here are consistent with the existing literature, with most repeatabilities ranging between 0.3 and 0.8 (Auer et al., 2016; Nespolo and Franco, 2007; Versteegh et al., 2008; White et al., 2013). Our repeatability of mass-adjusted metabolic rate, ranging between 0.3 and 0.4, is also consistent with earlier studies in birds, although perhaps on the lower range relative to that found in earlier zebra finch studies, which was between 0.3 and 0.6 (Careau et al., 2014; Rønning et al., 2005; Verhulst et al., 2006; Vézina and Williams, 2005). Two aspects of our study are likely to have contributed to this difference. Firstly, our dataset covers a larger time range (up to 5.5 years), which deflates trait repeatability (Auer et al., 2016; White et al., 2013). Secondly, our birds were housed outdoors and thus exposed to a wider range of environmental variation than birds housed indoors. Thus, the repeatability of our metabolic rate measurements is within the range one would expect based on earlier studies.

How environmental quality affects trait repeatability is not well known. Heritability, i.e. the proportion of phenotypic variance due to additive genetic effects, was shown to increase weakly but significantly with environmental quality (Charmantier and Garant, 2005; Visscher et al., 2008; but see Rowinski and Rogell, 2017). Hence, a positive association is sometimes expected between repeatability and environmental quality. We did in fact find the expected difference for BMR_m and SMR_m, but the error around our estimates was such that this difference was only marginally significant despite a considerable sample size. However, for body mass and SMR_m there was also an environmental effect on within-individual variance, being higher in the benign environment (significant for body mass, the trait with the largest sample size). This contrasts with the expectation for repeatability because, everything else remaining equal, large within-individual variance decreases repeatability. Indeed, the repeatability of body mass was independent of environmental quality because within- and between-individual variance both changed significantly and to the same extent. Our findings imply that there is no general prediction regarding the effect of environmental quality on trait repeatability.

Weak metabolic correlations: causes and implications

To the best of our knowledge, this study is the first to quantify the correlation between BMR_m and SMR_m. Intraspecific correlations between BMR (or BMR_m) and other measures of energy expenditure, such as DEE and maximum metabolic rate (MMR; which is a special case of SMR when measured at very low T_a because it is not sustainable) were often found to be weak in endothermic species (DEE: Careau et al., 2012; Fyhn et al., 2001; Meerlo et al., 1997; Speakman et al., 2003; Tieleman et al., 2008; Wiersma and Tinbergen, 2003; cold-induced MMR: Chappell and Bachman, 1995; Petit et al., 2013; Swanson et al., 2012; Vézina et al., 2006; Wiersma et al., 2007a; Zhang et al., 2015). Why these correlations are weak is not well known. BMR_m is largely determined by central organs, while insulation and T_b will in addition be important for energetic expenditure at sub-thermoneutral T_a (such as SMR_m, DEE and MMR; Daan et al., 1989; Daan et al., 1990; Suarez and Darveau, 2005; Vézina et al., 2006; Wiersma et al., 2012; Zhang et al., 2015). That there are different drivers of variation in BMR_m (central organ mass and cellular activity) and SMR_m (insulation and T_b) is likely to contribute to weakening the correlation between BMR_m and SMR_m. Here, we showed that individual differences in thermoregulation (T_b) in response to low temperature caused a low correlation between BMR_m and SMR_m and the same effect is likely to weaken correlations with DEE and MMR. There are, however, more drivers of variation for the weak correlation between BMR and DEE or MMR; in particular, additional variance due to variation in activity level is likely to be important. The extent to which thermoregulation explains the weak correlation between BMR and DEE can be verified by testing how much better SMR at ecologically relevant temperatures correlates with DEE or MMR than BMR.

Between-individual correlations between SMR_m12 and SMR_m26 were high, and this observation was confirmed by the random slope analyses. In contrast, between-individual correlations between BMR_m and SMR_m were low. This finding may be due to individual differences in conductance (heat loss over the T_b–T_a gradient; McNab, 1980), with better insulated individuals showing a weaker metabolic rate response to lower T_a. Alternatively, the heterogeneity in metabolic rate response may be due to variation in T_b response to lower T_a. Our data (Figs 6 and 7) indicate that at least part of the heterogeneity in metabolic rate response can be attributed to the latter effect. Unfortunately, our data prevent us from estimating conductance directly because SMR and T_b were measured at different times (night and morning, respectively). In European kestrels *Falco tinnunculus*, a food rationing-induced decline in T_b was substantially larger at night than in the morning (Daan et al., 1989), indicating the error introduced when calculating conductance using metabolic rate and T_b measured at different times. Hence, the correlation between BMR_m and SMR_m is low at least in part due to individual differences in T_b regulation, and

individual variation in conductance may have further contributed to this finding, but this remains to be tested.

BMR is often used to characterize energy consumption or minimum cost of self-maintenance of individuals or species. Our finding that BMR and SMR are poorly correlated raises the question whether BMR or SMR is most suitable for this purpose. When individuals are the unit of analysis, for example when relating an individual's minimum energy expenditure to life-history traits (e.g. Burton et al., 2011; Nilsson and Nilsson, 2016), SMR may be preferable because heat loss is an inevitable determinant of an individual's minimum levels of energy expenditure and animals spend much of their time at sub-thermoneutral T_a. Because SMRs at all sub-thermoneutral T_a correlate almost perfectly with each other (Table 2), it appears that individual differences in SMR are equally well characterized at any sub-thermoneutral T_a. However, when species are the unit of analysis, the problem is more intricate because species live at different T_a (Wiersma et al., 2007a,b, 2012). A possible solution might be to quantify SMR a standard number of degrees below the thermoneutral zone. Conversely, at the interspecific level, BMR and SMR may be well correlated, in which case using either BMR or SMR should make little difference for the results, but this needs to be verified.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: M.B., S.V.; Methodology: M.B., S.V.; Software: M.B.; Validation: M.B.; Formal analysis: M.B., S.V.; Investigation: M.B., S.V.; Resources: M.B.; Data curation: M.B., S.V.; Writing - original draft: M.B.; Writing - review & editing: M.B., S.V.; Supervision: S.V.; Project administration: M.B., S.V.; Funding acquisition: S.V.

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